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HISTORICAL, NOMENCLATURAL, AND DISTRIBUTIONAL NOTES ON TWO PACIFIC COAST KELPS: *LESSONIOPSIS LITTORALIS* AND *PLEUROPHYCUS GARDNERI* (PHAEOPHYCEAE, LAMINARIALES, ALARIACEAE)

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Abstract

The names of two eastern North Pacific kelps (Phaeophyceae, Laminariales, Alariaceae) were inadvertently validated by Josephine Tilden on labels to specimens distributed in the exsiccata "American Algae". Lectotypes for *Lessonia littoralis* and *Pleurophycus gardneri*, which concomitantly are the types of the names of the monospecific genera *Lessoniopsis* and *Pleurophycus*, respectively, are herein designated from among specimens housed in the Herbarium of the University of Minnesota, Tilden's home institution. *Lessoniopsis* ranges from Kodiak Island, Alaska, to the Big Sur coast of Monterey County, California, whereas *Pleurophycus* ranges from southeastern Alaska to Pt. Piedras Blancas, San Luis Obispo County, California. Molecular data suggest that both *Lessoniopsis* and *Pleurophycus* belong to the Alariaceae, a departure from their previous familial placements in the Lessoniaceae and Laminariaceae, respectively.

Key Words: W. G. Farlow, Laminariales, *Lessonia*, *Lessoniopsis*, *Pleurophycus*, DeAlton Saunders, W. A. Setchell, Josephine Tilden.

Lessoniopsis littoralis

As recounted by Setchell and Gardner (1903, p. 267), *Lessoniopsis littoralis* Farlow et Setchell ex Tilden was first brought to the attention of science by Elihu Hall of Oregon, who sent a specimen to William Gilson Farlow at Harvard. Farlow (1875, p. 355) assigned it tentatively to *Lessonia fuscescens* Bory (syntype localities: Concepción, Chile, and the Falkland Islands). Later, Farlow (1876, p. 707) assigned the Hall specimen to *L. nigrescens* Bory (type locality: Cape Horn). After having seen a living specimen at Monterey in 1885, Farlow decided that Hall's specimen represented an undescribed species of *Lessonia* for which he proposed the manuscript name *L. littoralis*. This name can be found on labels to specimens in the Farlow Herbarium (FH) or sent by Farlow to other herbaria. The species was still undescribed when William Albert Setchell, who had been appointed Professor of Botany at the University of California in 1895, first saw it in the field – at Cypress Point, Monterey Peninsula, in July 1896. In his notebook, under no. *1417*, Setchell wrote "*Lessonia litoralis* [using an alternative spelling of the epithet] Farlow mscr.", but on the labels to his specimens he wrote "*Lessonia litoralis* F. & S.". The use of "F. & S." for the authorship appears to follow Josephine Tilden's exsiccata, "American Algae" (fourth century, dated February 20, 1900), in which a description of "*Lessonia littoralis* Farlow and Setchell. Mss." is given on the label to no. *342*. The basis for this accreditation is unclear as there is no evidence that Farlow or Setchell had provided Tilden with pertinent information. In fact, Tilden had previously severed relations with Setchell (letter to Setchell dated November 21, 1898) because of the "unpleasant spirit" and "ungentlemanly tone" of his criticism of the first fascicle of her exsiccata.

On the label to no. *342*, Tilden gave credit to DeAlton Saunders for the determination. Saunders had recently returned from serving as botanist on the Harriman Alaska Expedition, which gave him the opportunity to observe and collect this kelp. An explanation of how Tilden came to describe the species can be found in a letter from Saunders to Setchell, dated March 1, 1900:

> "I was somewhat surprised on receiving Miss Tilden ['s] set [American Algae Century IV] that I had determined so many species. While I was working Christmas at Minneapolis she often showed me things that bothered her & I suggested that they look like so & so—That evidently constituted a determination in her mind. Thinking to save her a great deal of unnecessary blundering & perhaps the chagrin of redescribing your *Lessonia* I told her my understanding of it & suggested her writing you ... I believe her work for pure superficiality cannot be equalled."

Farlow was scarcely less critical. In a letter to Setchell dated March 12, 1896, with regard to the first fascicle of "American Algae", Farlow wrote:

> "Miss Tilden ['s] specimens are worse than any I ever saw except Kützing's... A good part of

FIG. 1. Lectotype of *Lessonia littoralis* Farlow et Setchell ex Tilden (MIN 3607).

FIG. 2. Lectotype of *Pleurophycus gardneri* Setchell et Saunders ex Tilden (MIN 3613).

the other numbers which I have examined are incorrectly named. I felt like writing a savage notice of the century but I concluded that it was better to say nothing. Whatever criticism emanates from Harvard is believed in a good part of the country to be merely ill natured jealousy of progressive Western botanists and any criticism, however just, excites sympathy for the person criticized and has no weight as criticism."

Whatever her shortcomings as a taxonomist, Tilden made significant contributions to phycology. She was a pioneer in the study of thermal algae in the United States. She founded the University of Minnesota Seaside Station at Port Renfrew on the west coast of Vancouver Island. She compiled and published a card index to phycological literature, "Index Algarum Universalis", popularly called the "Tilden Index", which remains useful despite being largely unknown or ignored by present-day taxonomists. She also published a somewhat idiosyncratic but thought-provoking text book, *The algae and their life relations* (Tilden 1935), a pioneer work in which classification was addressed with reference to pigmentation, food reserves, and evolutionary environmental changes.

Because no other collections were cited on the label, the specimens distributed as no. *342* in Tilden's "American Algae" constitute the type collection of *Lessonia littoralis*. This collection was made by Tilden on August 3, 1898, at Baird Point on the Strait of Juan de Fuca, Vancouver Island, British Columbia, Canada. Three specimens of this distribution are in the Herbarium of the University of Minnesota (MIN) while two are in the Herbarium of the University of California (UC), all so fragmentary as to validate Farlow's criticism of the quality of Tilden's collections. One specimen (MIN 3607), which lacks the exsiccata label but is otherwise labeled "*Lessonia littoralis* Farlow. Am. Alg. 342.", is somewhat more informative than the other four specimens seen in this study and is herein designated lectotype (Fig. 1). All other distributions of no. *342* are isotypes (isolectotypes). The name *Lessonia littoralis* must be accredited either to Tilden (when using an abbreviated format) or to Farlow et Setchell ex Tilden (when using an extended format), but not to Farlow et Setchell because Tilden wrote the diagnosis. The type locality has been incorrectly indicated as Cypress Point, Monterey Peninsula, by Smith (1944, p. 145) and Nicholson (in Abbott and Hollenberg 1976, p. 246).

Lessonia littoralis was made the type of a new genus, *Lessoniopsis* by Reinke (1903), thus restricting *Lessonia* to the southern hemisphere. *Lessoniopsis littoralis* (Tilden) Reinke is a cumaphyte, growing only in the most exposed rocky sites, usually just below *Postelsia palmaeformis* Rupr. in the lowermost intertidal and upper subtidal zones. It ranges from Kodiak Island, Alaska (Druehl 1970) southward to Kasler Point, Monterey County, California (*Silva 802* in UC).

Pleurophycus gardneri

Setchell and Saunders, independently from one another, recognized *Pleurophycus gardneri* Setchell et Saunders ex Tilden as an undescribed species representative of an undescribed genus of kelps. The first specimens available to Setchell were those collected in 1898 by N. L. Gardner, a high school teacher in Oak Harbor on the west coast of Whidbey Island, Washington. The alga that Setchell immediately recognized as undescribed is similar to *Laminaria*, with a single blade borne on a sturdy stipe, but unlike the latter genus, its blade has a midrib. For this alga Setchell proposed the manuscript name *Pleurophycus gardneri*. On June 26, 1899, Saunders collected the same kelp at Yakutat Bay, Alaska. In a letter to Setchell dated September 1, 1899, Saunders wrote:

> "It is a good thing for both of us that I stayed a week in Pudget Sound & collected with Mr Gardner. Otherwise I should have done you an injustice—I should have had the description of your *Pleurophycus* published under a different name."

Setchell then proposed joint authorship and Saunders hesitantly accepted the proposal. In subsequent correspondence, the place of publication was discussed, Saunders favoring the forthcoming results of the Harriman Expedition while Setchell favored a note intended for the journal *Zoe*. While Setchell and Saunders were dithering, Tilden published a valid description of this new genus and species under the name "*Pleurophycus gardneri* Setchell and Saunders Mss." (label to no. *346*, American Algae, fourth fascicle, February 20, 1900). As with *Lessonia littoralis*, Tilden came to publish the first description of this kelp with the inadvertent assistance of Saunders during his Minneapolis visit at Christmas time in 1899.

Setchell (1901) published a more complete description in the journal *Zoe*, which appeared early in 1901 (between February 15, when the editor, Mrs. Brandegee, sent proof to Setchell, and March 26, when Mrs. Weeks acknowledged receipt of a reprint from Setchell). The account of the algae of the Harriman Alaska Expedition (Saunders 1901) was published November 15, 1901. Plate LII in that account is a drawing of "an almost perfect specimen ... collected by Miss J. E. Tilden in Puget Sound". This specimen has not been located.

The specimens distributed by Tilden under no. *346* in both sets of "American Algae" housed

at UC and the set at MIN are predictably fragmentary. The specimen at Minnesota (MIN 3613) comprises a horizontal swath of a blade, a small piece of a stipe, and the base of a blade minus the holdfast. The specimens were collected by Tilden on May 28, 1898, at North Bay, San Juan Island, Washington, and determined by Saunders. Because no other collections are cited on the label, these specimens must be considered as constituting the type collection. No specimen in the Herbarium of the University of Minnesota was indicated by Tilden as the holotype. Therefore, no. *346* of "American Algae" (MIN 3613) is herein designated lectotype of *Pleurophycus gardneri* (Fig. 2). All other distributions of this number are isotypes (isolectotypes). The generic and specific names must be accredited either to Tilden (when using an abbreviated format) or to Setchell et Saunders ex Tilden (when using an extended format), but not to Setchell et Saunders (as has always been done in the past), because Tilden wrote the diagnosis. The type locality is San Juan Island and not Whidbey Island (as has been erroneously assumed by previous authors).

At the time when the known southern limit of *Pleurophycus gardneri* was Coos Bay, Oregon, Setchell and Gardner (1925, p. 607) speculated that "It possibly extends many miles further south, even to the coast of California." The first collection from California seems to be a plant obtained in the drift in Mendocino Bay on August 21, 1965, by E. K. Daniels (UC 1318218). Kjeldsen (1972) reported the finding of a large population on rocks at extreme low tide level at Fort Bragg, Mendocino County, and an isolated specimen from the drift at Salt Point, Sonoma County. VanBlaricom et al. (1986) studied subtidal populations of *Pleurophycus* off Pt. Sierra Nevada and Pt. Piedras Blancas in San Luis Obispo County, thus greatly extending the range southward. They also retrieved two thalli of *Pleurophycus* from the anchor upon departure from a site near Pt. Sur. *Pleurophycus* was later found growing on an unnamed bank near Pt. Sur (subsequently named Schmieder Bank) by a Cordell Expedition in 1989 (UC 1575256, 1575257) and was reported as forming a zone at depths of 30–45 m all along the coast of Monterey County from Carmel to Pt. Sur (Spalding et al. 2003).

Although the progression of records suggests a southward movement of this kelp, there is no reason to believe that the distribution in California has changed in recorded history.

Classification of *Lessoniopsis* and *Pleurophycus*

The numerous genera of kelps are held together in a single order, Laminariales, distinguished by a unique structural plan and a nearly unique life history that involves separate gametophytic and sporophytic generations. Gametophytes are very small filamentous thalli that undergo oogamous sexual reproduction. The thallus of the sporophyte is parenchymatous and comprises a holdfast, stipe, and blade, the latter two structures joined by a transitional meristematic zone. Sporangial sori are borne either on a central blade or on special lateral sporophylls. Whereas gametophytes show relatively little variation, there is an astonishing number of variations of the sporophyte, leading to the recognition of a large number of monotypic genera. In a long-standing but simplistic classification, longitudinal splitting of the meristem and the production of lateral sporophylls by the stipe immediately below the transition zone were cardinal points in the recognition of three families of Pacific coast kelps: Laminariaceae, without splitting or lateral sporophylls; Alariaceae, without splitting but with lateral sporophylls; and Lessoniaceae, with splitting but without lateral sporophylls. *Lessoniopsis* has a complex morphology that makes classification difficult. The meristem splits repeatedly to produce a very large number of narrow, ribbed, sterile blades, each blade subtended by 1–3 pairs of ribless sporophylls. This straddling of two families (Lessoniaceae and Alariaceae) was accommodated by Setchell and Gardner (1925) by placing the genus in its own tribe within the Lesssoniaceae, deciding on this family rather than the Alariaceae because the thallus of *Lessoniopsis* more closely resembles that of *Lessonia* than that of *Alaria*. Prior to the recognition of the Alariaceae and Lessoniaceae by Setchell and Gardner (1925), the Lessoniopseae had been established by Setchell (1912) as a tribe of Laminariaceae.

Pleurophycus, by contrast, has a simple form that apparently is not very different from *Laminaria*. Germann (1986), however, has shown that at the end of the growing season the blade abscisses, in contrast to other members of the Laminariaceae in which the old blade disappears progressively in response to senescence and abrasion by wave action in winter storms. After the blade has abscissed, the abscission layer is protected by an outgrowth of cortical cells, forming a scar that remains at the distal end of newly formed blades. Another unusual feature is the formation of sporangial sori on the midrib as well as on the wings of the blade.

Despite the distinct morphology of such genera as *Postelsia*, *Macrocystis*, and *Nereocystis*, the Laminariales show relatively little molecular diversity. Nucleotide sequence comparisons of various parts of the nuclear, chloroplast, and mitochondrial genomes of 42 species reveal unexpected groupings of genera within the Alariaceae-Laminariaceae-Lessoniaceae complex

(Lane et al. 2006). In the new alignment, both *Lessoniopsis* and *Pleurophycus* are included in the Alariaceae along with the traditionally placed members *Alaria* and *Pterygophora*. The presence of lateral sporophylls in *Lessoniopsis* is a character in agreement with *Alaria* and *Pterygophora*, but it is difficult to imagine the evolutionary transformation of *Pleurophycus* from an alarioid ancestor to its present-day laminarioid form.

The molecular-based Laminariaceae has an even more surprising circumscription. In addition to genera traditionally assigned to this family, it includes *Nereocystis, Macrocystis, Pelagophycus*, and *Postelsia*. The inclusion in the Laminariaceae of these four genera, which have traditionally been assigned to the Lessoniaceae, greatly narrows the breadth of the latter family, but molecular data supports the transfer of *Egregia* and *Eisenia* from their traditional placement in the Alariaceae to the Lessoniaceae, where they join the southern hemisphere genera *Lessonia*, *Ecklonia*, and *Eckloniopsis*. On the basis of molecular data, Lane et al. (2006) established a fourth family, the Costariaceae, comprising *Agarum*, *Costaria*, *Dictyoneurum*, and *Thalassiophyllum*. These familial realignments imply that longitudinal splitting in the transition region and the production of sporophylls are characters that have arisen more than once, thus increasing the difficulty of writing diagnoses at the family level.

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